SIMPLE AND CONDITIONAL VISUAL DISCRIMINATION WITH WHEEL RUNNING AS REINFORCEMENT IN RATS

IVER H. IVERSEN

UNIVERSITY OF NORTH FLORIDA

Three experiments explored whether access to wheel running is sufficient as reinforcement to establish and maintain simple and conditional visual discriminations in nondeprived rats. In Experiment 1, 2 rats learned to press a lit key to produce access to running; responding was virtually absent when the key was dark, but latencies to respond were longer than for customary food and water reinforcers. Increases in the intertrial interval did not improve the discrimination performance. In Experiment 2, 3 rats acquired a go-left/go-right discrimination with a trial-initiating response and reached an accuracy that exceeded 80%; when two keys showed a steady light, pressing the left key produced access to running whereas pressing the right key produced access to running when both keys showed blinking light. Latencies to respond to the lights shortened when the trial-initiation response was introduced and became much shorter than in Experiment 1. In Experiment 3, 1 rat acquired a conditional discrimination task (matching to sample) with steady versus blinking lights at an accuracy exceeding 80%. A trial-initiation response allowed self-paced trials as in Experiment 2. When the rat was exposed to the task for 19 successive 24-hr periods with access to food and water, the discrimination performance settled in a typical circadian pattern and peak accuracy exceeded 90%. When the trial-initiation response was under extinction, without access to running, the circadian activity pattern determined the time of spontaneous recovery. The experiments demonstrate that wheel-running reinforcement can be used to establish and maintain simple and conditional visual discriminations in nondeprived rats.

Key words: wheel-running reinforcement, discriminative control, conditional discrimination, matching to sample, trial-initiation response, circadian rhythms, key press, rats

---

Rodent wheel running is a versatile response that can be studied in relation to a variety of parameters, such as time of day and feeding (e.g., Eikelboom & Mills, 1988; Looy & Eikelboom, 1989). Wheel running can also be studied as an operant that produces access to food (e.g., Henton & Iversen, 1978; Iso, 1996; Skinner & Morse, 1958), as a schedule-induced behavior (e.g., White, 1985), as a competing behavior (e.g., Henton & Iversen, 1978; Iversen, 1985), and as a reinforcer (e.g., Premack, 1965).

Wheel-running reinforcement affords an opportunity to examine methods to study behavior maintained by reinforcers that do not require deprivation. Customarily in animal research, food or water deprivation is used to ensure that the subject readily consumes the food or water when presented so that it may serve as a reinforcer and hence maintain the behavior that produces access to it. Studies with food and water reinforcers in nondeprivation conditions have primarily examined intake as a function of consumption costs in closed economies (e.g., Mathis, Johnson, & Collier, 1995, 1996). Deprivation is not ordinarily used with human subjects in clinical or educational settings. Therefore, educators and therapists must find reinforcers for which deprivation is not defined or controlled (such as praise or games); see for example, Fisher et al. (1992) and Pace, Ivancic, Edwards, Iwata, and Page (1985). Animal models of nondeprivation reinforcement conditions are therefore of potential interest for research with human subjects.

Several prior studies have demonstrated that wheel running can effectively maintain operant behavior in rats and other rodents (e.g., Belke, 1996, 1997; Belke & Heyman, 1994; Collier & Hirsch, 1971; Iversen, 1993b; Kagan & Berkun, 1954; Mazur, 1975; Premack, 1962; Premack, Schaeffer, & Hundt, 1964; Tierney, Smith, & Gannon, 1983; Timberlake & Allison, 1974). For example, Iversen (1993b) demonstrated that lever pressing could be maintained under fixed-ratio (FR), fixed-interval (FI), and variable-ratio (VR) schedules with contingent access to running in brief 4- to 6-s access periods. The op-

erant behavior was often maintained in schedule-appropriate patterns. Most prior work with wheel-running reinforcement primarily sought to answer theoretical questions about the nature of reinforcement (e.g., Premack, 1962, 1965; Timberlake & Allison, 1974). But wheel-running reinforcement also has practical applications. For example, using rats, Tepper and Weiss (1986) studied the effects of ozone exposure on lever pressing maintained by access to wheel running. Belke (1997) used wheel-running reinforcement to examine the effects of amphetamine on operant behavior. Because deprivation conditions may interact with the agent being examined, wheel-running reinforcement has the advantage that the subject need not be either food or water deprived. An additional advantage of wheel-running reinforcement is that it can maintain operant behavior in long sessions in a closed environment that permits the emergence of characteristic circadian patterns of the operant behavior as well as free feeding and drinking.

Apparently, no previous study has attempted to determine whether wheel-running reinforcement might maintain a simple discriminated operant, let alone a conditional discrimination. The purpose of the present experiments was to explore techniques that may render wheel running a reinforcer that is sufficient to establish and maintain stable operant behavior under discriminative control by visual stimuli in rats that are neither food nor water deprived.

Discriminative control brings operant behavior beyond mere strengthening and maintenance by setting certain stimulus occasions under which the behavior is reinforced and other stimulus occasions under which the behavior is not reinforced. Under one stimulus, say a light turned on, the target operant is reinforced, whereas under another stimulus, say the light turned off, the operant is not reinforced. For example, when the light-on and light-off periods alternate in some manner, the operant behavior eventually settles into a corresponding on-off pattern. Skinner (1938) argued that the discriminated operant is an important demonstration of how an aspect of the subject's environment can set the occasion for and guide or cue operant behavior. The discriminated operant is thus very important for both basic and applied re-

search (Dinsmoor, 1995; Harrison, 1991). One use of discrimination procedures, for example, is to determine which training and stimulus conditions are necessary to establish when the subject "detects" the stimuli (i.e., when the stimuli control the behavior). In animal research, food and water reinforcers are commonly used in situations involving discriminative control or conditional discriminations (for examples, see Harrison, 1991; Mackay, 1991). Wheel-running reinforcement would considerably expand the use of discrimination procedures to situations in which food and water reinforcers cannot readily be used because the deprivation may interact with the drug or toxin to be tested.

The present study extends previously established techniques for wheel-running reinforcement described in Iversen (1993b). Thus, the operant response produced access to running in a wheel for periods that approximate the duration of consumption of food or water reinforcers in common operant paradigms with food or water deprivation (e.g., 5 to 10 s). The experiments progressed from a simple one-response stimulus on-off discrete-trial procedure in Experiment 1, to a go-left/go-right two-stimulus procedure in Experiment 2, to a conditional discrimination (matching-to-sample) procedure in Experiment 3. To determine whether local deprivation of wheel running affects discrimination performance, intertrial intervals (ITI) were manipulated in Experiment 1. To determine whether a self-paced trial distribution would facilitate discrimination performance, a trial-initiation response was introduced in Experiments 2 and 3. Previous experiments have shown that operant performance maintained by wheel-running reinforcement can be sustained for several consecutive days and eventually develops a circadian pattern (Iversen, 1993b). To extend the study of circadian rhythms of discrimination performance using wheel-running reinforcement, Experiment 3 explored the maintenance of the conditional discrimination performance over several successive 24-hr sessions with food and water available in the apparatus.

GENERAL METHOD

Subjects

In each experiment, the subjects were experimentally naive female Long Evans rats, 3

to 4 months old at the start of the experiment. The rats were neither food nor water deprived and had free access to both food and water in individual Wahmann home cages (18 cm wide, 24 cm deep, and 18 cm high). A 12:12 hr light/dark cycle operated in the colony room. Food and water were available in the experimental chamber for Rat 5 in Experiment 2 and in the last condition of Experiment 3.

Apparatus

The running wheel was 15.5 cm wide with a circumference of 103.7 cm. The running surface consisted of 2-mm steel bars spaced every 8.5 mm. The wheel could turn in either direction. Rotation of the wheel was recorded as one of three magnets mounted equidistant on the circumference of the wheel passed a reed relay mounted on the support of the wheel. This method of recording wheel running did not differentiate the direction of wheel rotation. A modified relay served as a remotely controlled rim brake. The brake could release the wheel instantly; at a speed of one revolution per second, the brake could bring the wheel to a stop in about 0.5 s. The wheel was suspended on one side. The other side was a stationary wall with three transparent nose keys, a lever, a food cup, and an aperture that provided access to a waterspout.

The three nose keys (1.5 cm diameter) with a center-to-center distance of 6 cm, were aligned horizontally 20 cm above the running surface. Each key could be lighted from behind by a 14-VDC steady or blinking (at 0.1-s intervals) green light. In Experiment 1, an aluminum ring (1 cm wide) surrounded the center nose key. A custom-made touch sensor recorded paw and nose contact with this ring. The lever (2 cm by 2 cm) was placed 3 cm to the left of the midline of the wall and 5 cm above the running surface. A lever press was recorded as a 3-mm depression of the lever with a force greater than 0.1 N. A food cup (3 cm by 2 cm by 1 cm) was mounted 5 cm to the right of the lever. Noyes 45-mg food pellets were delivered into this cup in the last condition of Experiment 3. An aperture was located between and 2 cm above the level of the lever and the food cup; a waterspout appeared in this aperture for Rat 5 in Experiment 2 and in the last condition of Experiment 3. Contacts with the food cup and the waterspout were recorded with custom-made touch sensors.

The running wheel apparatus was enclosed in a sound-attenuating cubicle with a fan and masking noise. Sessions were conducted in darkness except for the stimuli that appeared on the nose keys. Programming and recording were accomplished by a combination of solid-state equipment and a Tandy Model 102 computer.

Procedure

All experiments followed the same general procedure of free access to running, establishment of reliable running when the brake was released (here called reinforcer control), and then contingent access to running. To establish reinforcer control, brief periods with access to running alternated with periods without access to running. First, 1-min periods with free access to running alternated with 5-min periods with no access to running. The access period was then reduced gradually to 30 s, to 15 s, and then to shorter periods. Reinforcer control was considered established when running occurred in all access periods and within 1 to 2 s after release of the brake. The distinct sound from the relay that controlled the brake proved sufficient to control prompt onset of running when the brake was released.

In Experiments 1 and 2 as well as the first part of Experiment 3, sessions were scheduled at about the same time of the day for each subject (between 9:00 a.m. and 4:00 p.m.), and each subject had two or three sessions each week. In the last part of Experiment 3, sessions were continuous for several days.

EXPERIMENT 1

Experiment 1 sought to determine whether wheel-running reinforcement can sustain a discriminated operant. Access to running in the wheel was made contingent on pressing a nose key when the key was lit. To determine whether the discrimination could be sustained with intermittent reinforcement, an FR 10 schedule was introduced gradually when the key was lit. Because the discrimination was not particularly well maintained at first, an attempt was made to improve the

performance by increasing the local deprivation of wheel running by prolonging the ITI.

Method

Two rats were used. After five 60-min sessions of unrestricted access to running, access was restricted gradually to 9-s periods over 10 sessions to establish reinforcer control. Automated shaping of pressing the center nose key was accomplished in Condition 1 by progressing from a simple, minimal-effort touch response to pressing the nose key. By first reinforcing merely touching the ring around the key, it was expected that the rats would eventually press the key because of response generalization. The key was lit with a steady light for up to 60 s with a variable ITI averaging 2 min (range, 20 to 240 s). When the key was lit, a touch on the metal ring around the key produced wheel-running reinforcement and terminated the light on the key. The response requirement of touching the ring was increased from FR 1 to FR 10 over six sessions. When the nose key was lit, a single press on the nose key throughout these six sessions could also produce wheel-running reinforcement. That is, access to the wheel was gained either by pressing the key once or by touching the ring around the key according to schedule (FR 1 to FR 10). Nose-key pressing was acquired for both rats with this procedure, and manual shaping was not used.

In all subsequent sessions, wheel-running reinforcement was contingent only on pressing the nose key; touching the ring around the nose key was merely recorded. The schedule for nose-key pressing during the discriminative stimulus (S^D) was changed from FR 1 to FR 10 over three sessions. The FR 10 was maintained for the remainder of the experiment. Once FR 10 had been reached, the ITI was increased to 5 min for six sessions (Condition 2). The ITI was then increased to 10 min for one session and then to 15 min for six sessions (Condition 3). Last, the ITI was set to 10 min for six sessions (Condition 4). In Conditions 3 and 4, the trial duration was set to a maximum of 60 s. If the FR was not completed during a trial, the light extinguished after 60 s and the FR was reset. Sessions were terminated after 20 trial opportunities had occurred. Thus, session durations varied with the ITI such that, for ex-

ample, sessions with a 15-min ITI lasted about 5 hr. In all conditions, ITIs were variable, with 10 different intervals ranging from one fifth of the average ITI to two times the average.

Results

Both rats acquired the nose-key response with the automated training procedure in Condition 1. However, the response was poorly maintained, with mean latencies to the light (time from light onset to the first nose-key press) of 55 and 84 s for Rats 1 and 2, respectively. In addition, the response rate was low and about the same both during the light (S^D) and during the ITI. Table 1 presents the summary data. An attempt was made to determine whether an increase in local deprivation of running, by increasing the ITI, might enhance the effectiveness of the reinforcer. Also, to help differentiate the response rates in the presence of the S^D and the ITI, the response requirement was increased to FR 10 (Condition 2). The response rate increased during S^D and remained low during the ITI for both rats, but the latency of responding to the light remained very long. When the ITI was increased further to 15 min (Condition 3), the latency of responding to the light decreased and both rats essentially stopped responding during the ITI. However, both rats missed several trials; thus, Rat 1 responded to only 20% of the trials, and Rat 2 responded to 87% of the trials. When the ITI was set back to 10 min in Condition 4, Rat 1 responded to 51% of the trials, and Rat 2 responded to all trials. In addition, the latency of responding to the light shortened further for both rats; latencies in the 1- to 5-s range began to emerge for Rat 2. The response rate in S^D increased further for Rat 2 to 34.3 responses per minute, with a rate of nearly zero in the ITI.

Figure 1 shows a sample of the final discrimination performance in a segment of an event record for Rat 2; the performance for Rat 1 was similar except that some trials did not have any responses and thus ended after 60 s. The discrimination is indicated by the fact that pressing the key (lowest trace) occurred only during the light (top trace). The fourth trace shows touching the metal ring that surrounded the key. The touch necessarily occurred simultaneously with the nose-key response but also occasionally occurred in

Table 1

Mean latency to the S^D, response rate during S^D, response rate during the ITI, and running speed (full wheel revolutions per second) during reinforcer access in Experiment 1. Means are based on the last three sessions of each condition. RC indicates reinforcer control with restricted access to running. The time unit for the ITI is minutes.

Rat	Condition	Latency (seconds)	S^D rate (responses per minute)	ITI rate (responses per minute)	Running speed (revolutions per second)
1	RC				0.35
	FR 1, ITI 2	55	1.7	1.3	0.59
	FR 10, ITI 5	51	7.5	1.0	0.37
	FR 10, ITI 15	40[a]	9.8[a]	0.4	0.27
	FR 10, ITI 10	32[a]	8.6[a]	0.3	0.35
2	RC				0.47
	FR 1, ITI 2	84	1.3	1.8	0.26
	FR 10, ITI 5	70	5.9	0.5	0.38
	FR 10, ITI 15	24[a]	17.7[a]	0.2	0.42
	FR 10, ITI 10	12	34.3	0.3	0.48

[a] Data calculation excludes trials without responding.

the absence of this response (such as the single instance seen here during one ITI). Both rats ran in all access periods.

The running speed during access periods for sessions with response-contingent access to running gradually increased during the experiment for Rat 2 but decreased for Rat 1 (see Table 1). Before reinforcer control and discrimination performance were established, the overall running rates (running divided by session duration) with free access were 352 and 304 revolutions per hour for Rats 1 and 2, respectively.

Discussion

Experiment 1 demonstrates that both rats acquired a simple discrimination of responding to the light with access to running as the only contingent outcome. However, the discrimination was poorly maintained for Rat 1. An increase in the ITI improved the performance for Rat 2 by decreasing the latency and increasing the response rate. But a subsequent ITI decrease further improved the performance of Rat 2, suggesting that continued exposure to the procedure was more important than the increase in the ITI. The improvement in performance was modest for Rat 1; however, discrimination was evident because responding to the key occurred almost exclusively during trials. Nevertheless, for both rats the latencies to respond to the light were considerably longer than those routinely observed for food or water reinforcers, which

typically generate latencies in the 0.5- to 3-s range in this laboratory under similar simple discrimination procedures.

EXPERIMENT 2

In Experiment 2, a go-left/go-right discrimination was set up using visual stimuli on two nose keys. When both keys showed steady lights, pressing the left key produced access to wheel running, and when both keys showed blinking lights, pressing the right key produced access to running. When wheel running reinforced responding on simple schedules in Iversen (1993b), performance was well maintained on FR and VR schedules but less well on an FI schedule. One difference between ratio and interval schedules is that the subject can increase the reinforcer rate on ratio schedules by responding more, whereas in the case of interval schedules increasing the response rate does not increase the reinforcer rate (once the response rate is above a certain minimum). In the present Experiment 1, the opportunity to run was timed by the ITI. Experiment 2 explored the effects of making the discrimination task more like a ratio schedule by allowing the subject to control the timing of the opportunity to run. Thus, Experiment 2 introduced a trial-initiation response in an attempt to improve the discrimination performance. In essence, the procedure became a chained schedule; discrimination performance was reinforced by access to running, and lever pressing was re-
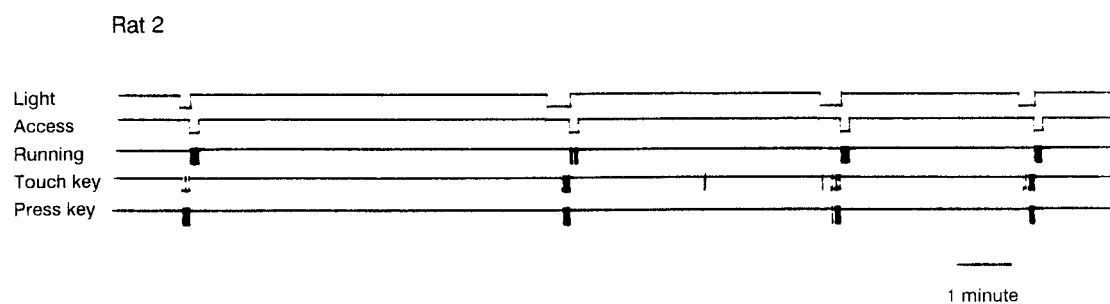
Rat 2

Fig. 1. Representative sample of an event record showing light on or off, access to running, running (each third of a revolution displaced the event pen), contact with the metal ring that surrounded the nose key, and nose-key presses. Access to running in the wheel was contingent on pressing the nose key under an FR 10 when the key was lit. Data are for Rat 2 and illustrate the final discrimination performance in Experiment 1.

inforced by onset of the discriminative stimuli. The discrimination was reversed after acquisition of stimulus control.

Method

Three rats were used. After three 60-min sessions with free access to running, reinforcer control was established over six sessions by gradually reducing the access period to 8 s.

Preliminary training. Because each subject had pressed the nose keys on occasion during sessions that established reinforcer control, shaping of nose-key pressing was considered unnecessary. A trial started when either the left or the right side key was lit. The light would appear on either key with equal probability. A response to the lit key extinguished it and released the brake to the wheel. Pressing an unlit key during a trial terminated the trial without access to wheel running. Trials were separated by a variable ITI. For the first session, the key remained lit until a response occurred, and the ITI was 10 s (range, 5 to 15 s). For the next 10 sessions, trials terminated after 15 s if no response occurred, and the ITI was 1 min for the first two sessions and then 2 min for the next eight sessions (range, 20 to 240 s). Pressing an unlit key during the ITI delayed the onset of the next trial by 15 s. To establish a trial-initiating response, trial onset was made contingent on a lever press for the next five sessions. (Because lever pressing had occurred sporadically during prior sessions, shaping of lever pressing was considered unnecessary.) The keys remained dark until a lever press occurred. The ITI duration was thus no longer timed by a clock but was now under control of the sub-

ject's lever-pressing behavior. Trials were initiated by a lever press for the remainder of the experiment. Preliminary training lasted 16 sessions; each session was 60 min long.

Discrimination training. The final task was a go-left/go-right discrimination. With a steady light on both keys, a press on the left key produced wheel-running reinforcement. With a blinking light (0.1-s periods) on both keys, a press on the right key produced reinforcement. Pressing the incorrect key extinguished the lights without reinforcement. Following a reinforced trial, the next trial had an equal probability of having either steady or blinking lights, with the only restriction that the same key could not be correct on more than four consecutive trials.

This final discrimination task was approached using a fading procedure that increased the intensity of the stimulus on the incorrect key from absent to full intensity. For one session, only one key was lit during a trial; either the left key was lit with a steady light and a response to that key was reinforced, or the right key was lit with a blinking light and a response to that key was reinforced. Pressing an unlit key terminated the trial. Then, the light on the incorrect key was first very dim and was then gradually made brighter over nine, six, and five sessions for Rats 3, 4, and 5, respectively. (The changes in light intensity were accomplished between sessions by placing a gradually smaller resistor in series with the light on the incorrect key.) Next, a correction procedure was introduced that repeated a trial until a response on the correct key occurred. The final discrimination was maintained for nine sessions. An unsig-

naled 10-s timeout followed a response to the incorrect key during the last four, six, and four of these sessions for Rats 3, 4, and 5, respectively. When a timeout was in effect, the first lever press after the timeout produced the next trial.

Stimulus reversal. The stimuli for the go-left/go-right discrimination were reversed; the right key was correct when both keys showed a steady light, and the left key was correct when both keys showed a blinking light. Otherwise, the procedure was the same as during the final sessions before the reversal. Stimulus reversal lasted 10, 6, and 8 sessions for Rats 3, 4, and 5, respectively.

During preliminary training, discrimination training, and stimulus reversal, sessions lasted 2 hr for Rats 3 and 4. For Rat 5, sessions also lasted 2 hr in preliminary training; thereafter, sessions lasted 16 to 24 hr and were scheduled overnight with a full day between sessions. Water was freely available and several biscuits of chow were placed in the food cup before these sessions for Rat 5.

Results

During preliminary training with only one stimulus appearing on one of the side keys, with 2-min ITIs, a large proportion of the trials passed without a nose-key response to any key (the light extinguished after 15 s without a response); the percentages of trials with a nose-key response were 65%, 45%, and 72%, for Rats 3, 4, and 5, respectively. When the trial-initiation response was introduced, the percentage of trials with a response to the lit key increased to 100% for all rats within two sessions. In addition, the latency of responding to the lit key shortened considerably from a mean of about 22 s without the trial-initiation response to about 2 s when the trial-initiation response was introduced. Furthermore, by the end of preliminary training, the trial-initiation response had resulted in a considerable increase in the frequency of trials from about 30 per hour (set by the 2-min ITI) to 70, 58, and 120 trials per hour for Rats 3, 4, and 5, respectively. Thus, the light controlled responding much more effectively when the subject produced the stimulus.

Figure 2 shows each subject's percentage of trials with a press on the correct key for each session of discrimination training and stimulus reversal. Data represent full sessions for
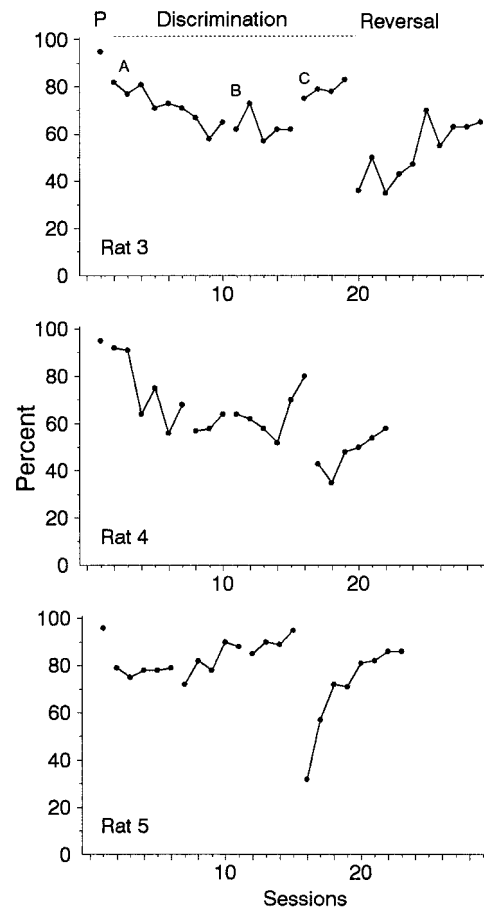

Fig. 2. The percentage of correct responses in the go-left/go-right discrimination for each session after preliminary training in Experiment 2. The first session (marked P) had only the correct key lit. In sessions marked A, the intensity of the light on the incorrect key was increased gradually over sessions. At B, both keys were lit with the same intensity and a correction procedure was introduced. A 10-s timeout was introduced at C. The stimuli were reversed during reversal sessions.

Rats 3 and 4 and the first 2 hr of each session for Rat 5. As the intensity of the light on the incorrect key was gradually changed from no light to a light of the same intensity as on the correct key (via the fading procedure), the percentage correct gradually decreased from near 100% (with only the correct key lit) to approximately 70% for Rats 3 and 4 and 80% for Rat 5. By the end of discrimination training with full intensity on both keys, the percentage correct had increased to about 80% for Rats 3 and 4 and 90% for Rat 5.

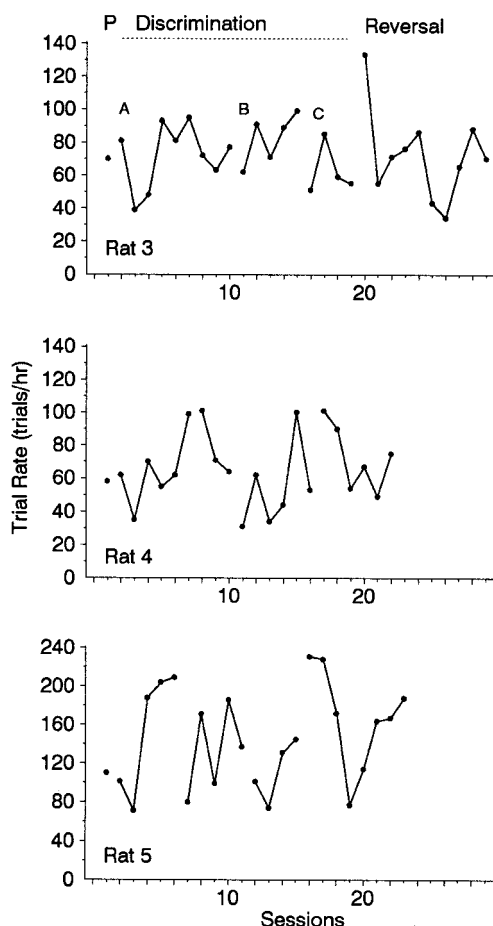After stimulus reversal, the percentage cor-

Fig. 3.   The rate of response-initiated trials in the go-left/go-right discrimination for each session after preliminary training in Experiment 2. See Figure 2 for details. Notice that the *y*-axis scale is different for Rat 5 because of its relatively high trial rate.

increased considerably on the first session immediately after stimulus reversal for all rats and also on the second session for Rats 4 and 5. This increase in trial rate exceeded any prior rate seen for Rats 3 and 5. The considerable drop in percentage correct and hence in reinforcement rate right after stimulus reversal apparently facilitated the trial-initiation response.

To illustrate the typical flow of trial initiation, discrimination performance, and wheel running, Figure 4 presents a segment of an event record showing 10 consecutive trials from the last session of discrimination training for Rat 5. The first two trials beginning on the left had steady light on both keys; Rat 5 pressed the left key in both cases and immediately ran in the wheel when the brake was released. Trial 3 had blinking lights on both keys, and a press on the right key was reinforced. After a response to the incorrect key in Trial 8, there was no opportunity to run, and several lever presses occurred during the 10-s timeout.

As shown on the event record, latencies to respond to the nose keys when they were lit were generally short. Based on an analysis of the last three sessions of discrimination training, the median latency was 0.9, 0.6, and 0.9 s for Rats 3, 4, and 5, respectively. The median latencies did not differ systematically for left and right keys and for correct and incorrect responses. Approximately 80% of all latencies were shorter than 1.5 s for all rats. During both discrimination training and reversal, all rats responded on the keys on all trials.

Wheel running. Table 2 presents the overall rate of running (running divided by session duration) and the speed of running during wheel access (running divided by total reinforcer duration). Data are presented for the last three sessions of each condition. Running speed was not defined for the free-access condition. Overall run rate is not presented for reinforcer control because the opportunity to run was paced by a clock. In discrimination and in stimulus reversal, Rat 3 ran about as much overall as during free access, whereas Rat 4 ran less than in free access. Rat 5, in contrast, ran considerably more in discrimination and especially in the reversal condition than under free access. Thus, across rats, the amount of running in the free condition

rect first dropped considerably below 50% and then approached the same level as before the reversal for Rats 3 and 5. For Rat 4, the percentage correct also dropped, but increased only slowly and did not reach the same level as before the reversal. Regrettably, due to laboratory logistics, further sessions could not be scheduled for Rat 4.

Figure 3 presents the rate of trials for each session of discrimination training and stimulus reversal. Because of the trial-initiation procedure, the rate of trials was determined entirely by the subject's behavior. During discrimination training, the trial rate ranged from 30 to 100 per hour for Rats 3 and 4 and 70 to 210 per hour for Rat 5. The trial rate
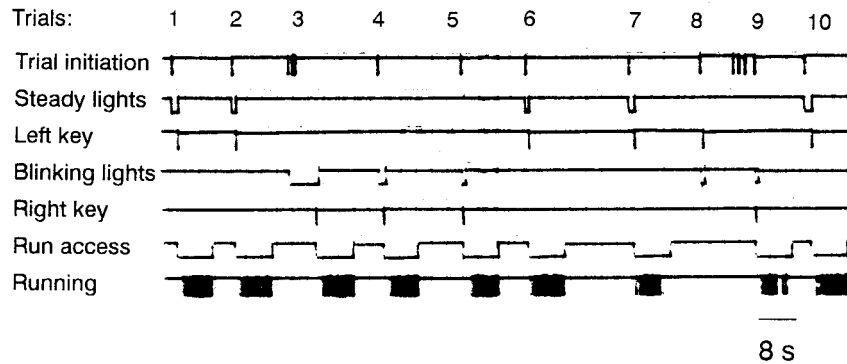
Rat 5

Fig. 4. Representative sample event record illustrating the flow of events during sessions in Experiment 2 for Rat 5. For wheel running, each third of a revolution displaced the event pen.

did not predict the amount of running in the contingent conditions.

The running speed during access to running increased from reinforcer control to subsequent conditions for all rats and increased from discrimination to reversal for Rats 4 and 5 but decreased in reversal for Rat 3. Although Rat 5 produced the highest trial rate and the largest overall run rate during discrimination, Rat 5's run speed was less than that of the other 2 rats during discrimination.

Discussion

Experiment 2 established a more complex discrimination involving two stimuli and two responses. The percentage correct dropped and then increased (for 2 of 3 rats) when the discrimination was reversed. Thus, the results showed that wheel-running reinforcement can sustain the acquisition, maintenance, and reversal of a visual go-left/go-right discrimination. The acquisition was facilitated using traditionally successful methods such as fading in the incorrect stimuli, a correction pro-

Table 2

Overall rate of running and running speed during access to running in Experiment 2. Free is free access to running (running speed is not defined in this condition), RC is reinforcer control (overall running rate is not given because access to running is not controlled by the subject). Data are shown as the mean of the last three sessions of each condition and the individual sessions (in parentheses).

Rat	Condition	Overall running rate (revolutions per hour)	Running speed (revolutions per second)
3	Free	239 (202, 254, 261)	
	RC		0.38 (0.33, 0.43, 0.38)
	Discrimination	271 (239, 194, 381)	0.88 (0.96, 0.87, 0.80)
	Reversal	239 (218, 280, 219)	0.63 (0.67, 0.63, 0.60)
4	Free	340 (343, 326, 350)	
	RC		0.34 (0.30, 0.38, 0.35)
	Discrimination	239 (185, 239, 292)	0.86 (0.92, 0.80, 0.82)
	Reversal	254 (251, 169, 342)	0.92 (0.95, 0.83, 0.97)
5	Free	238 (263, 210, 245)	
	RC		0.36 (0.35, 0.34, 0.42)
	Discrimination	344 (256, 363, 413)	0.54 (0.48, 0.52, 0.63)
	Reversal	735 (653, 731, 820)	0.73 (0.70, 0.75, 0.73)

cedure that repeated trials with a response to the incorrect key, and a timeout following a response to the incorrect key (see Harrison, 1991). Because the present experiments sought mainly to establish whether or not discrimination could be obtained at all with wheel-running reinforcement, the separate influence of these techniques for acquisition of the discrimination was not assessed. However, the experiment showed that the method of having self-paced trials by adding the trial-initiating response facilitated the discrimination performance during preliminary training; the latency to the stimuli decreased, no trials were missed, and the rate of trials increased. Probably because of the trial-initiating response, the latency to respond was considerably shorter in Experiment 2 than in Experiment 1 and was now within the range of latencies seen for food and water reinforcers used in similar procedures in this laboratory.

On the first session of stimulus reversal, the trial rate increased compared to that of most sessions prior to the reversal. Because of the drop in reinforcer rate caused by frequent responses to the incorrect key during the first session of reversal, this increase in trial rate is probably related to the increase in response rate seen early in extinction sessions under various schedules of reinforcement (Ferster & Skinner, 1957), that is, the so-called extinction burst.

EXPERIMENT 3

Methods that establish conditional discriminations serve an important role in animal research (e.g., Mackay, 1991). Experiment 3 attempted to determine whether wheel-running reinforcement might be sufficient to sustain a conditional discrimination, such as matching-to-sample performance. With steady and blinking lights in a three-key procedure, matching-to-sample performance has been established previously in rats using food reinforcement (Iversen, 1993a). Using the same procedure in the present experiment but with wheel-running reinforcement, a steady or blinking light appeared on the center of three keys. After a press to the center key, the two side keys lit up, with one key showing a steady light and the other a blinking light; a press to the side key that matched

the center key produced access to wheel running as the reinforcer. Because Experiment 2 showed that a trial-initiating response may facilitate discrimination performance maintained by wheel-running reinforcement, lever pressing also served such a function in the present experiment. Thus, a press on the lever started the trial by illuminating the center key with the sample stimulus. To examine the circadian pattern of the matching-to-sample performance once it had developed, sessions were continuous over a 19-day period with food and water available in the equipment.

Method

Initially 2 rats were used, but 1 rat was removed from the experiment because of poor performance. After two sessions with free access to running (Condition 1), wheel access was restricted gradually to 15-s periods over 10 sessions (Condition 2) using the same procedure of reinforcer control as in Experiments 1 and 2.

Pretraining. In Condition 3 (one session), all three keys were lit continuously, and a response to either key released the brake to the wheel for 15 s. Both rats responded to the keys, and shaping of nose-key pressing was not necessary. In Condition 4 (two sessions), the three keys were lit one at a time with steady light in mixed order. A response to a lit key released the brake and extinguished the keylight. To establish a trial-initiating response, a single lever press produced trial onset. In the absence of lever pressing, trials were separated with variable ITIs that averaged 5 min (range, 1 to 10 min). This procedure proved to be sufficient to establish lever pressing as a trial-initiating response. In Condition 5 (two sessions), a trial began with illumination of the center key with either a steady light or a blinking light with a period of 0.1 s. A response to the center key lit one side key with the same stimulus as on the center key, and the center key remained lit while the other side key remained dark. A response to the lit side key then released the brake and extinguished the lights. The wheel access duration was reduced to 12 s, which was maintained for the rest of the experiment. Also in Condition 5, the ITI timer was suspended so that all trials were produced by a lever press. In pretraining, sessions usually lasted about 2

hr and were scheduled every other day at about the same time of day.

Matching-to-sample procedure. In Condition 6 (Sessions 1 through 40), a lever press lit up the center key with steady or blinking light. A response to the center key turned on both side keys, and the center key remained lit. One side key showed the same stimulus as the center key, and the other side key showed the nonmatching stimulus. A response to the side key with the matching stimulus released the brake and extinguished all keylights. A response to the nonmatching side key extinguished all keylights and produced an unsignaled 10-s timeout from Session 1 to Session 8. Lever pressing during the timeout had no effect other than being recorded; the first lever press after the timeout produced the next trial. A correction procedure was in effect in Sessions 1 through 21; a trial that did not result in reinforcement was repeated until a response to the correct key occurred. A trial was terminated automatically (all keylights extinguished) after 40 s if a response to the center key had not occurred or if a response to either side key had not occurred (after a response to the center key), and the same trial was repeated. Additional procedural details are given along with the results.

Up to Session 17, sessions usually lasted about 2 to 6 hr. From Session 18 to Session 40, the session duration was extended to 12 to 24 hr by keeping the rat in the equipment overnight with free access to water and several biscuits of rat chow in the food cup. To allow the rat to feed freely and to enable recording of food retrieval, 45-mg Noyes food pellets were delivered into the food cup contingent on completion of five touches of the food cup (FR 5) during Sessions 39 and 40; in Session 39 a handful of pellets was placed in the food cup, which proved to be sufficient to establish cup contact as a food-producing response.

In Condition 8, the matching-to-sample procedure was maintained while the rat was kept in the running-wheel equipment continuously for 19 days (Days 1 to 19). Food was available on the FR 5 schedule of cup contact, and water was freely available. Food and water were replenished (in dim light), and the equipment was checked and cleaned without removing the rat at a different time each day when the rat was inactive. The equipment was kept dark except for the lights that appeared on the keys during trials. Thus, no attempt was made to entrain the circadian rhythm to lights (e.g., Terman, 1983).

Results

Acquisition. Rat 7 acquired the matching-to-sample performance but Rat 6 did not. After reinforcer control and preliminary training as for Rat 7, Rat 6 had 17 sessions with the matching-to-sample procedure but the accuracy never exceeded 70%. The experiment was terminated at that point for Rat 6 because it completed a mere 30 to 40 trials in most sessions compared to several hundred trials for Rat 7. Data are therefore presented for Rat 7 only; however, some results are presented for Rat 6 at the end of the Results section.

The upper part of Figure 5 shows, for the first 40 sessions, accuracy as the percentage of trials with a response to the correct key and preference as the percentage of trials with a response to the right side key; the lower part of Figure 5 shows the session duration and the rate of response-initiated trials.

Accuracy slowly increased from near 50% to above 80% over the first 22 sessions (a total of 8,250 trials had been completed by Session 22). After 15 sessions with marked preference for the right side key, the percentage of trials with the left key correct was increased to induce a reversal of preference for the left side key (see Iversen, 1993a). The percentage of trials with the left key correct was set to 75% for Sessions 16, 18, and 20 (A in Figure 5); during Session 21 the percentage was set to 67% (B). The preference for the right side key diminished after these preference-correction sessions, and accuracy increased from below 70% to above 80%. By Session 32, preference began to reverse in favor of the left side key. When the percentage of trials with the right side key correct was increased to 67% in Sessions 35 and 38 (C in Figure 5), the key preference shifted in the corresponding direction. The mean latency to respond to the center key after it was lit by the trial-initiating response was 0.9 s, and the mean latency to respond to a side key after the center key had been pressed was 0.8 s (data are from Sessions 39 and 40).

Because the rate of response-initiated trials fluctuated considerably in the 2- to 6-hr ses-
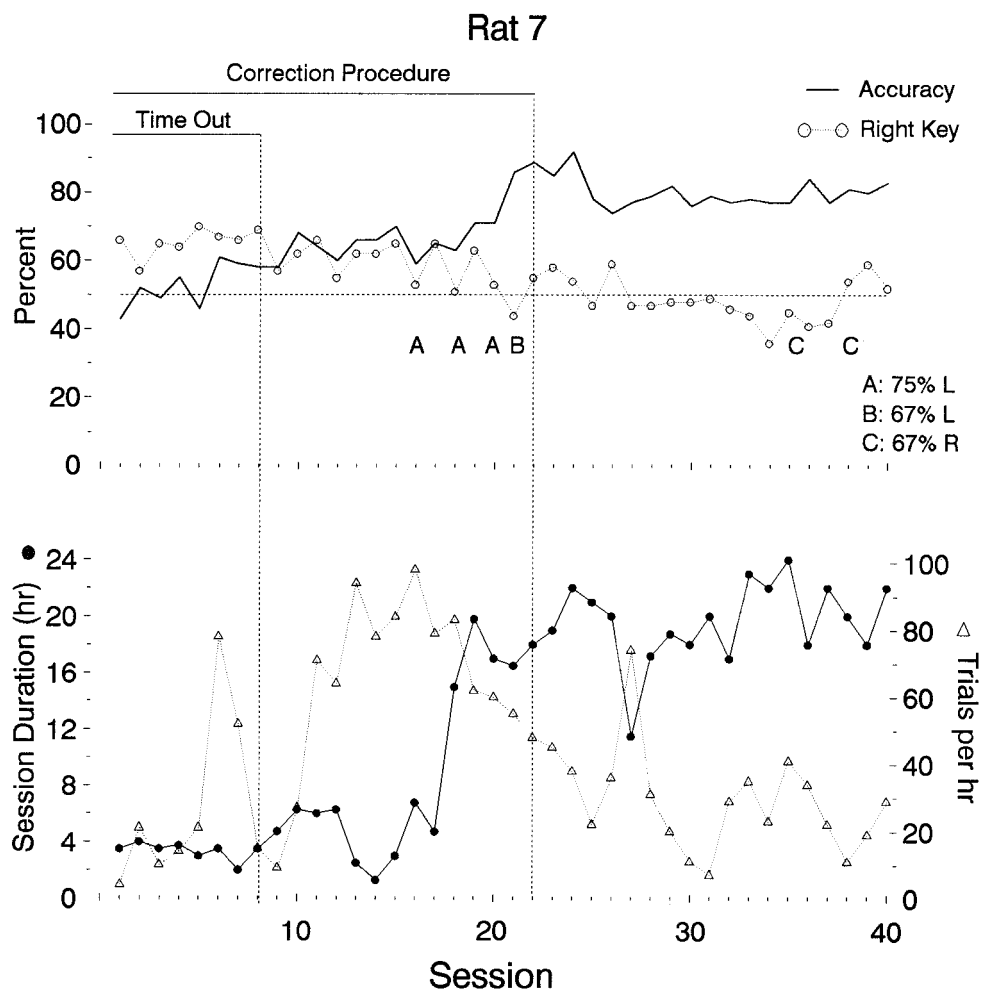
Rat 7

Fig. 5.   The upper display shows the accuracy of the matching-to-sample performance and the percentage of trials with preference for the right side key for Sessions 1 through 40 in Experiment 3. Procedural conditions are indicated along the top, and the letters A through C refer to sessions in which the trial distribution was altered to counteract the key preferences (see text). The lower display shows the session durations and the rate of response-initiated trials.

sions, the session duration was extended to 12 to 24 hr from Session 18 to possibly cover a time period marked by a higher level of activity. Although the trial rate per session still varied, more trials were now completed each session. In most 12- to 24-hr sessions, Rat 7 would complete 50 to 100 trials at a rate of two to three trials per minute right after being placed in the apparatus. Then several hours would pass with few if any trials initiated before the trial rate would again be high for several hours.

Circadian patterns. To facilitate examination of shifts in activity over time, data are commonly double plotted in studies of circadian

rhythms (e.g., Terman, 1983). Accordingly, Figure 6 presents a double plot of the rate of response-initiated trials for each hour of each day when Rat 7 was kept in the equipment. For example, the second row shows data for Day 1 followed by data for Day 2; the third row shows data for Day 2 followed by data for Day 3, and so forth. To analyze whether matching accuracy varied with time of day and the rate of trial initiation, the trial rate data are coded with respect to accuracy.

After some variability on Days 1 and 2, a pattern of several consecutive hours with high rates of trial initiation followed by several consecutive hours with zero or very low
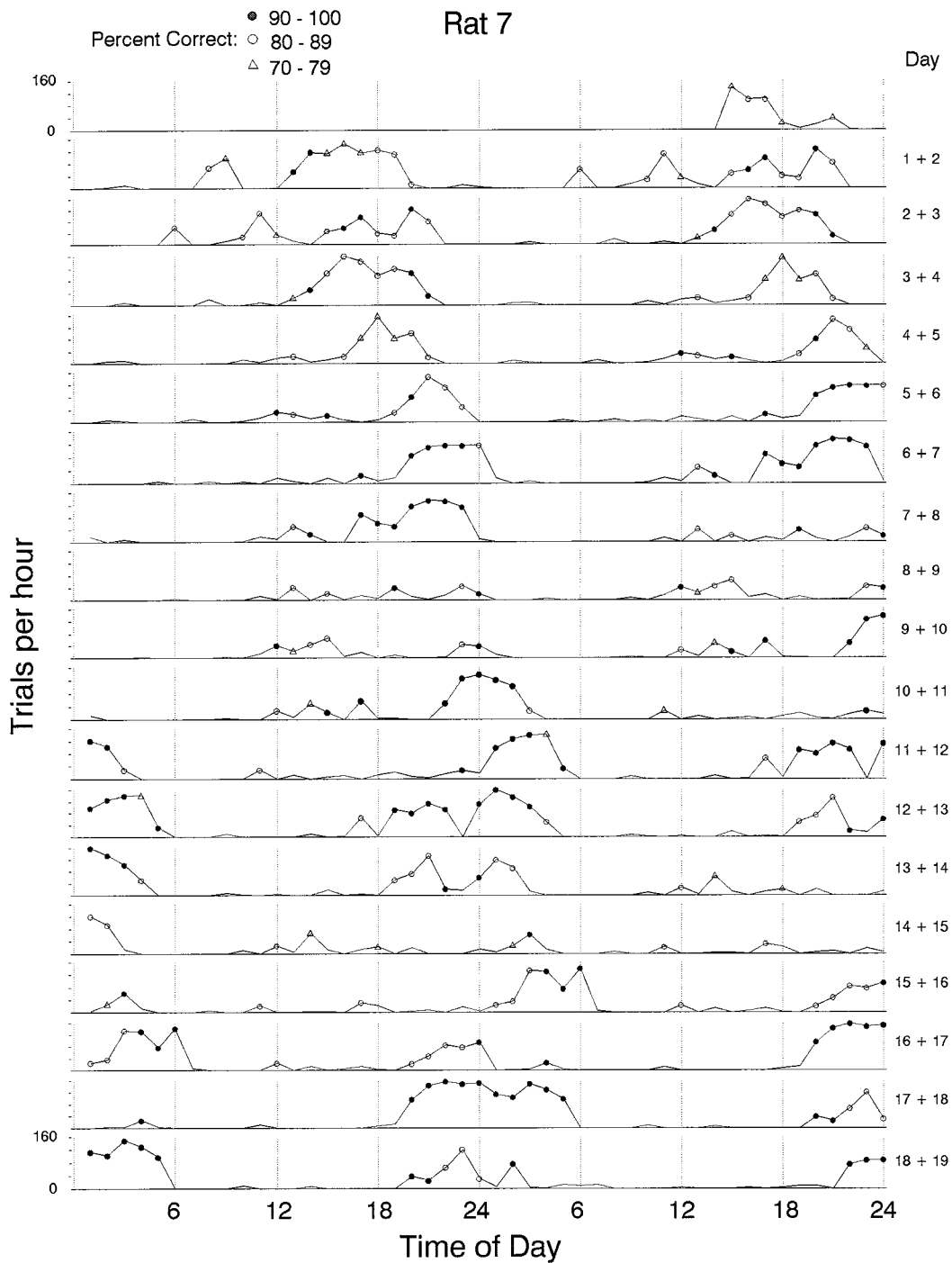
Fig. 6. The rate of response-initiated trials is shown for 19 successive days. Rat 7 was placed in the equipment on the afternoon of the day preceding Day 1 and remained in the equipment throughout the 19-day period. Water was freely available during sessions. Touching the food cup produced food pellets under an FR 5 schedule. Lever pressing initiated trials, which presented a matching procedure with access to wheel running for a 12-s period as reinforcement. Data points are coded for percentage correct of the matching performance when the trial rate was higher than 10 trials per hour. Data are double plotted to illustrate how the temporal activity pattern shifted over the 19-day period.

rates characterized almost all days. The time of day marked by trial activity clearly shifted over the succeeding days. During Days 1 through 4, Rat 7 was most active between 1:00 p.m. and 9:00 p.m. During Days 15 through 19, after about 2 weeks in the equipment, the most active period was between 8:00 p.m. and 4:00 a.m. A general suppression in trial rates was evident on Days 8 and 9 and Days 14 and 15.

Performance accuracy generally increased over the 19-day period. High accuracy (90% or higher) most often occurred during periods with high trial rates. Thus, on days with a high level of activity (e.g., Days 6 and 7), accuracy generally was higher than on days with a low level of activity (e.g., Days 8 and 9). The longest period of peak performance occurred on Day 17 and spanned 10 hr with performance continuously at 90% or higher (per hour) for a total of 1,289 trials. During this period, the longest stretch of trials without a single response to the incorrect key was 197 and lasted 80 min.

The spontaneous alternation between trial activity and no trial activity offers an opportunity to examine whether wheel running might be a stronger reinforcer after running has been absent for some time than when running has occurred for several hours. That is, does the local deprivation of wheel running engendered by absence of the trial-initiating response affect the percentage correct once the trial-initiating response reappears? Commonly, the rate of response-initiated trials rose slowly during the activity periods. In addition, the percentage correct was generally higher in the middle of an activity period than in the beginning of the period. Thus, absence of wheel running for several hours did not seem to promote a surge in trial activity or a high percentage correct, either of which would have led to a relatively higher rate of opportunities to run. The data are more consistent with the view that running may become more effective as a reinforcer after several periods of access to running (i.e., reinforcer strength may build up during a period of high activity).

Eating and drinking occurred in two patterns. During the extended periods with little or no trial activity, eating would occur on occasion in 4- to 9-min uninterrupted bouts of high rates of pellet retrieval (about five pellets per minute) followed by a bout of water drinking usually lasting 1 to 2 min. During periods marked by high rates of trial activity, Rat 7 would on occasion stop the stream of trials to collect a single pellet, which was occasionally followed by a brief 20- to 30-s bout of drinking. The rate of pellet retrieval varied from 0.02 to 1.0 pellets per minute during periods of high activity.

Extinction of the trial-initiation response. After midnight on Day 19, the running wheel was made freely available for a 12-hr period to determine the influence on the operant behavior of free access to the reinforcer. Rat 7 ran continuously in bouts of 10 to 15 min separated by long periods (5 to 30 min) of inactivity. Lever pressing initiated trials at a rate of about five presses per hour, but trials were usually not completed. Rat 7 was then removed from the equipment for 3 hr and then was returned for a 2-day examination of extinction of the trial-initiation response. The wheel was locked continuously, and lever pressing did not initiate illumination of the center key; responses to the unlit nose keys accomplished nothing. Food and water were available as in prior continuous sessions.

Figure 7 shows the rate of lever pressing for each hour of the extinction period. Notice that the *y*-axis scale differs from that of Figure 6 because of the much lower trial-initiation rate in extinction. Lever pressing occurred immediately as the rat was placed in the apparatus. Thereafter lever pressing occurred roughly at the same time of day that trials had occurred during Days 17, 18, and 19 (i.e., between 7:00 p.m. and 6:00 a.m.). Notice that on the 2nd day of extinction, lever pressing occurred as frequently as, if not more frequently than, it did during the 1st day and roughly within the same time block. That is, 12 hr of extinction on the 1st day did not diminish what sometimes has been called spontaneous recovery on the following day (Rat 7 emitted 197 lever presses on the 2nd day from 6:00 p.m. to 8:00 a.m.).

The extinction period afforded an opportunity to examine whether the previously obtained dual pattern of pellet retrieval depended on the trial activity. That is, would the consistent low rate of pellet retrieval, which had occurred concurrently with trial activity, still occur when trials were prevented? The low rate of pellet retrieval, which previously
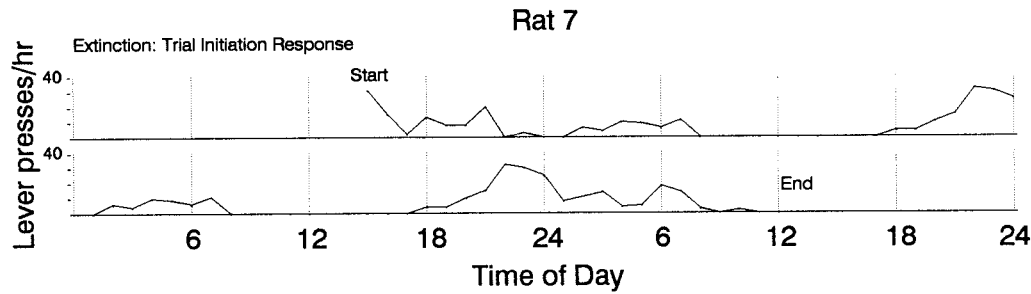
Rat 7

Extinction: Trial Initiation Response

Fig. 7. The rate of lever pressing over a 36-hr extinction session in which lever pressing did not initiate trials (access to running was prevented). Food and water were available as in prior sessions with trial access (see caption to Figure 6). Notice that the *y*-axis scale is different from that in Figure 6 because the rate of lever pressing was lower in the extinction session than in the prior sessions.

had occurred concurrently with trial activity, was practically abolished during the 2 days with extinction. Instead, long bouts of continuous pellet retrieval, at a rate of about five pellets per minute, occurred more often than during sessions with trial activity. The results therefore indicate that the trial activity had influenced the pattern of feeding during the previous sessions (Days 1 through 19). Although the pattern of eating was different during the two extinction sessions, the overall consumption of food was similar to that
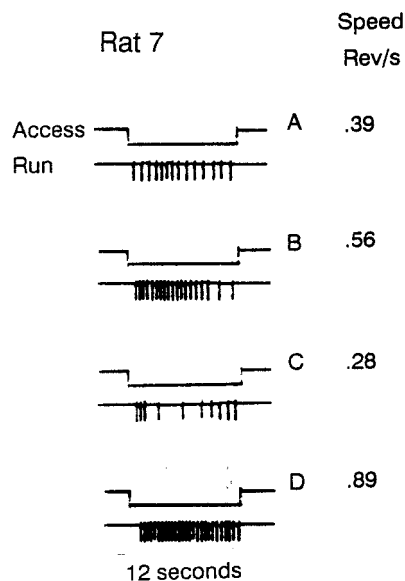

Fig. 8. Sample segments of event records illustrating four different patterns of wheel running during the 12-s access periods. Speed of running is indicated for each sample. Each pen displacement corresponds to one third of a revolution. Samples were taken from the first 50 reinforcers in Session 38.

found in the previous continuous sessions with wheel-running reinforcement.

Wheel running. The speed of running (number of revolutions divided by total reinforcer time) gradually increased over the course of the experiment. At the first and last sessions of reinforcer control, the speeds were 0.26 and 0.36 revolutions per second, respectively. For Sessions 1, 10, 20, 30, and 40, the speeds were 0.40, 0.43, 0.53, 0.47, and 0.52 revolutions per second, respectively. During Sessions 1 through 40, the lowest running speed for one session was 0.32 and the highest was 0.59 revolutions per second.

To illustrate the pattern of running during individual reinforcer periods, Figure 8 presents samples of event records showing running during the access period. The speed of running was analyzed for the first 50 reinforcers in Session 38, and it ranged from a low of 0.28 to a high of 0.89, with a median of 0.56 revolutions per second. Notice the prompt onset of running as soon as the brake was released, which was characteristic for practically all access periods. The most common patterns of running were a fixed pace through the 12-s period (A in Figure 8), a negative acceleration (B), irregular speed (C), or a very high speed (D). To give an impression of the possible speed of running and the distance covered by running, Rat 7 ran 933 cm (30.9 feet) in the single 12-s period marked D in Figure 8.

Measurement of running speed during continuous sessions was compromised because sessions were not defined by taking the subject in and out of the apparatus. However, a pragmatic session definition was the time

period between daily inspection and cleaning of the apparatus. The mean running speed during wheel access, as assessed in this manner, ranged from 0.41 to 0.61 revolutions per second over the 19-day period shown in Figure 6. Interestingly, the two lowest daily running speeds occurred for the time periods that corresponded to low trial activity. Thus, from 2:00 p.m. on Day 8 to 3:00 p.m. on Day 9, the running speed was 0.41 revolutions per second; similarly, from 2:00 p.m. on Day 14 to 2:00 p.m. on Day 15, the running speed was 0.42 revolutions per second. Conversely, the highest running speed occurred on days with considerable trial activity. For example, from 2:00 p.m. on Day 17 to 11:00 a.m. on Day 18, the running speed was 0.59 revolutions per second.

The overall amount of running (total distance run) was impressive on days with considerable trial activity. Thus, for the previously highlighted 10-hr peak performance on Days 17 and 18, the total distance run from 2:00 p.m. on Day 17 to 11:00 a.m. on Day 18 (which covered this 10-hr period) was 8,926 m (5.5 miles).

Rat 6. One difference between the 2 rats in the early sessions was that Rat 6 did not increase running speed during sessions with reinforcer control as did Rat 7 and as did the rats in Experiments 1 and 2 and the rats in Iversen (1993b). Also, running speed was erratic from session to session and from reinforcer to reinforcer during sessions with the matching-to-sample procedure. Conceivably, this lesser control of running during the access period was responsible for the poor control of the trial-initiating response and the matching performance for Rat 6.

Discussion

The experiment demonstrates that wheel-running reinforcement can sustain acquisition and maintenance of matching-to-sample performance at an accuracy in excess of 90%. The data indicate that matching-to-sample performance with wheel-running reinforcement can be maintained over extended time periods without the need to arrange for any kind of deprivation. The local deprivation of running engendered by several hours of inactivity each day did not seem to produce the highest rates of trial initiation or percentage correct once the rat commenced trial activity.

On the contrary, hours with the highest rates of trial activity and percentage correct usually followed hours with trial activity rather than hours without trial activity.

With continuous exposure to the apparatus for a 19-day period, performance quickly settled in a circadian pattern of several hours of trial activity separated by several hours of no activity. Peak performance consisted of up to 10 hr of continuous matching-to-sample performance at an accuracy of 90% or higher each hour. No lights in the apparatus marked time of day. Nonetheless, the pattern of trial activity slowly shifted about 10 hr over the 19-day period. This shift in activity is similar to shifts reported for unconstrained wheel running in female rats in continuous no-light situations (Wollnik & Turek, 1988). A general suppression in trial rates and percentage correct was evident on Days 8 and 9 and Days 14 and 15. For female rats, the estrous cycle influences general activity in periods of about 5 days. Estrous level was not obtained in the present experiment. However, the pattern of trial activity in the present experiment is consistent with known patterns of wheel running in female rats. In general, activity is highest on the day of estrus and lowest for 1 or 2 days after the estrus day (Wollnik & Turek, 1988). The consistent pattern of the discrimination performance established in the present experiment expands the domain of tasks that can be used to study the circadian rhythm of operant behavior (e.g., Terman, 1983).

The pattern of eating was influenced by the trial activity. Eating occurred in two patterns, a low rate (0.2 to 1.0 pellets per minute) concurrently with trial activity, or a high rate (about five pellets per minute) in uninterrupted (4 to 9 min) bouts when trial activity was absent. When trial activity was abolished during two extinction sessions, the low-rate eating pattern disappeared. Thus, the experimentally induced confinement of running to response-initiated 12-s periods interacted with the feeding pattern. Bouts of eating lasting several minutes would likely interfere with the opportunity for wheel running during periods with a high rate of trial activity. The intermittent feeding that occurred within several hours of high-rate trial activity apparently maintained food intake while the momentary interference of pellet retrieval on trial activity was reduced to the minimum of

retrieval of a single pellet, which lasted a mere 5 to 10 s, every other minute or so.

When Rat 7 was weighed at the end of the experiment, its weight was practically identical (5 g higher) to that immediately before the continuous sessions, indicating that the subject self-regulated feeding and drinking during the 19-day period, even though considerable time was spent in trial activity. The large scale competition between trial activity and feeding places circadian patterns of operant behavior within the more general framework of behavioral interactions that are seen in a variety of operant conditioning paradigms (e.g., Henton & Iversen, 1978). In addition, the reciprocal relation between feeding and running is consistent with reports of activity-based anorexia in rats, which may occur for some combinations of food deprivation and wheel-running access (Beneke, Schulte, & Vander-Tuig, 1995). By engaging in only limited feeding for periods up to 10 hr while engaging in high-rate trial activity, the rat essentially induces some degree of food deprivation, which in turn may determine when the rat shifts from trial activity to long bouts of feeding. Regrettably, only 1 of 2 subjects produced reliable data in Experiment 3. Therefore, the reported discrimination performance and interactions between feeding and trial activity may be somewhat limited in generality.

Nonetheless, the occurrence of consistent response patterns over several weeks, even with only 1 subject, suggests that the technique of wheel-running reinforcement may be very useful as a baseline for studies of visual conditional discrimination performance. Toxins, drugs, and other compounds may have effects on discrimination performance that are revealed only under continuous sessions.

In matching-to-sample procedures, the sample stimulus is customarily placed on the center key of the three response keys, as in the present experiment. However, the performance may not be maintained when the same stimuli are relocated (Iversen, 1997; Iversen, Sidman, & Carrigan, 1986) suggesting that the term *matching* may not be an appropriate label without further demonstrations that the sample does control the selection of the comparisons. In the present experiment, the term

matching to sample is thus used entirely to describe the procedure.

GENERAL DISCUSSION

The present experiments demonstrate that wheel running in nondeprived rats is a sufficient reinforcer to establish and maintain simple and conditional visual discriminations. The results thus extend the domain of traditional methods of discrimination (e.g., Harrison, 1991; Mackay, 1991) to a natural reinforcer that does not require any form of deprivation or special conditions. Allowing rats to freely feed and drink concurrently with discrimination tasks that are maintained solely by wheel-running reinforcement opens up the arena for studies of a variety of parameters that have effects that extend over time. Customary food and water reinforcers are not suitable for conditions with extended exposure because satiation influences the operant behavior in addition to the studied variables. Wheel-running reinforcement does not seem to be subject to the same local satiation factors that influence food- and water-reinforced operant behavior. Particularly impressive was the finding in Experiment 3 that wheel running can maintain discrimination performance almost continuously over several hours; the longest period of continuous trial activity lasted 10 hr with more than 100 trials completed each hour. Even with food or water deprivation, it is unlikely that one could maintain such extended work periods in rats using food or water reinforcement.

Although an access period of a fixed short duration (e.g., 10 s) sets a necessary condition for local restriction of running, it is not clear that extended local deprivation of running makes running a more potent reinforcer. For example, in Experiment 1, a prolonged ITI up to 15 min, which technically increased the local deprivation of running, did not improve the discrimination. Similarly, in Experiment 3, the self-paced absence of running for several hours did not make wheel running a more potent reinforcer when trial activity began again. These data are indirectly supported by one study in which Looy and Eikelboom (1989) showed that, with free access to wheel running, rats ran *less* after a 10-day deprivation of wheel running than before. When a trial-initiating response was

added in Experiment 2, the rate of trials increased above that previously set by the experimenter-specified ITI, and the discrimination performance improved immediately. In addition, in Experiment 3, the best discrimination performance was in fact obtained during long bouts of trial activity. In combination, these data suggest that, for wheel-running reinforcement with short access periods, the best performance is obtained when trials can occur close together. The trial-initiating response allows the subject to regulate the temporal pattern of running. Without the trial-initiating response, the rats missed several trial opportunities in Experiments 1 and 2.

More broadly, the results support the recommendation that self-paced responding may enhance the reinforcing efficacy of reinforcers that are presumably weak because deprivation cannot be done or is ineffective. At first, the data from Experiment 1 were not particularly encouraging regarding the potential use of wheel running as a reinforcer in discrimination procedures. ITIs were prolonged more and more, under the assumption that the resulting enhanced local deprivation would make wheel running more potent as a reinforcer. As Experiment 2 demonstrated, the opposite manipulation of providing more opportunities for running by introducing the trial-initiation response facilitated the discrimination performance. Thus, the ''motivational'' characteristics of wheel-running reinforcement may be quite different from the characteristics of reinforcers for which the subject is deprived, such as food and water. For reinforcers generated from biologically necessary commodities, increases in the ITI usually will improve performance, whereas self-paced trial spacing may satiate the subject quickly and thus contribute to deterioration of performance. For reinforcers generated from biologically unnecessary commodities (e.g., activity and sweets), engagement in the reinforcing activity appears to be a setting condition for the operant performance that generates the reinforcer. Thus, the roughly gradual increases in trial rate and percentage correct within extended periods of trial activity seen in Experiment 3 suggest that densely scheduled opportunities to run may make running a more and more effective reinforcer as more and more run bouts follow each other. At some point, trial activity begins to decline and eventually ceases completely for hours. Whether the subject is then satiated with running or is responding according to the circadian clock cannot be determined without further study. The trial-initiating response introduced in Experiments 2 and 3 essentially kept the ITIs very short. Again, further studies are needed to determine whether the trial-initiating response is effective only because it shortens the ITI or whether other variables play a role. For example, the trial-initiating response places the subject at the same spatial location with respect to the visual stimuli when the trial starts, thus preventing trial onset when the subject is engaging in irrelevant behavior (Henton, 1981).

Wheel-running reinforcement may offer a unique opportunity to study continuous exposure to extinction conditions. Experiment 3 showed that even after complete cessation of the trial-initiating response on the 1st day of extinction, this response returned in so-called spontaneous recovery exactly at the same time on the following day, with no external cues, resulting in a second extinction curve. Thus, even when the operant has been absent for hours, it still may not be extinguished. With customary reinforcers made of biologically necessary commodities such as food and water, extinction sessions cannot be conducted repeatedly without providing some form of access to the reinforcer, usually in the period between extinction sessions. With wheel-running reinforcement, the subject can be exposed to an unlimited number of extinction sessions without any adverse physiological effects resulting from the continued deprivation of the reinforcer. The circadian pattern of operant behavior in extinction appears to be an entirely unexplored area of research.

REFERENCES

Belke, T. W. (1996). The effect of a change in body weight on running and responding reinforced by the opportunity to run. *The Psychological Record, 46,* 421–433.

Belke, T. W. (1997). Running and responding reinforced by the opportunity to run: Effect of reinforcer duration. *Journal of the Experimental Analysis of Behavior, 67,* 337–351.

Belke, T. W., & Heyman, G. M. (1994). A matching law analysis of the reinforcing efficacy of wheel running in rats. *Animal Learning & Behavior, 22,* 267–274.

Beneke, W. M., Schulte, S. E., & Vander-Tuig, J. G. (1995). An analysis of excessive running in the development of activity anorexia. *Physiology and Behavior, 58,* 451–457.

Collier, G., & Hirsch, E. (1971). Reinforcing properties of spontaneous activity in the rat. *Journal of Comparative and Physiological Psychology, 7,* 155–160.

Dinsmoor, J. A. (1995). Stimulus control: Part I. *The Behavior Analyst, 18,* 51–68.

Eikelboom, R., & Mills, R. (1988). A microanalysis of wheel running in male and female rats. *Physiology and Behavior, 43,* 626–630.

Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement.* New York: Appleton-Century-Crofts.

Fisher, W., Piazza, C. C., Bowman, L. G., Hagopian, L. P., Owens, J. C., & Slevin, I. (1992). A comparison of two approaches for identifying reinforcers for persons with severe and profound disabilities. *Journal of Applied Behavior Analysis, 25,* 491–498.

Harrison, J. M. (1991). Stimulus control. In I. H. Iversen & K. A. Lattal (Eds.), *Techniques in the behavioral and neural sciences: Vol. 6. Experimental analysis of behavior* (Part 1, pp. 251–299). Amsterdam: Elsevier.

Henton, W. W. (1981). Kupalov conditioning: Molecular control of response sequences. *The Psychological Record, 31,* 489–509.

Henton, W. W., & Iversen, I. H. (1978). *Classical conditioning and operant conditioning: A response pattern analysis.* New York: Springer-Verlag.

Iso, H. (1996). Operant conditioning of wheel-running behavior in rats. *Japanese Journal of Animal Psychology, 46,* 41–60.

Iversen, I. H. (1985). Restricted access to collateral behavior affects operant behavior on variable-interval schedules. *The Psychological Record, 35,* 411–424.

Iversen, I. H. (1993a). Acquisition of matching-to-sample performance in rats using visual stimuli on nose keys. *Journal of the Experimental Analysis of Behavior, 59,* 471–482.

Iversen, I. H. (1993b). Techniques for establishing schedules with wheel running as reinforcement in rats. *Journal of the Experimental Analysis of Behavior, 60,* 219–238.

Iversen, I. H. (1997). Matching-to-sample performance in rats: A case of mistaken identity? *Journal of the Experimental Analysis of Behavior, 68,* 27–45.

Iversen, I. H., Sidman, M., & Carrigan, P. (1986). Stimulus definition in conditional discriminations. *Journal of the Experimental Analysis of Behavior, 45,* 297–304.

Kagan, J., & Berkun, M. (1954). The reward value of running activity. *Journal of Comparative and Physiological Psychology, 47,* 108–110.

Looy, H., & Eikelboom, R. (1989). Wheel running, food intake, and body weight in male rats. *Physiology and Behavior, 45,* 403–405.

Mackay, H. A. (1991). Conditional stimulus control. In I. H. Iversen & K. A. Lattal (Eds.), *Techniques in the behavioral and neural sciences: Vol. 6. Experimental analysis of behavior* (Part 1, pp. 301–350). Amsterdam: Elsevier.

Mathis, C. E., Johnson, D. F., & Collier, G. H. (1995). Procurement time as a determinant of meal frequency and meal duration. *Journal of the Experimental Analysis of Behavior, 63,* 295–311.

Mathis, C. E., Johnson, D. F., & Collier, G. H. (1996). Food and water intake as functions of resource consumption costs in a closed economy. *Journal of the Experimental Analysis of Behavior, 65,* 527–547.

Mazur, J. E. (1975). The matching law and quantifications related to Premack's principle. *Journal of Experimental Psychology: Animal Behavior Processes, 1,* 374–386.

Pace, G. M., Ivancic, M. T., Edwards, G. L., Iwata, B. A., & Page, T. J. (1985). Assessment of stimulus preference and reinforcer value with profoundly retarded individuals. *Journal of Applied Behavior Analysis, 18,* 249–255.

Premack, D. (1962). Reversibility of the reinforcement relation. *Science, 136,* 255–257.

Premack, D. (1965). Reinforcement theory. In D. Levine (Ed.), *Nebraska symposium on motivation* (Vol. 13, pp. 125–165). Lincoln: University of Nebraska Press.

Premack, D., Schaeffer, R. W., & Hundt, A. (1964). Reinforcement of drinking by running: Effect of fixed ratio and reinforcement time. *Journal of the Experimental Analysis of Behavior, 7,* 91–96.

Skinner, B. F. (1938). *The behavior of organisms.* New York: Appleton-Century-Crofts.

Skinner, B. F., & Morse, W. H. (1958). Fixed-interval reinforcement of running in a wheel. *Journal of the Experimental Analysis of Behavior, 1,* 371–379.

Tepper, J. S., & Weiss, B. (1986). Determinants of behavioral response with ozone exposure. *Journal of Applied Physiology, 60,* 868–875.

Terman, M. (1983). Behavioral analysis and circadian rhythms. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behavior* (Vol. 3, pp. 103–141). London: Wiley.

Tierney, K. J., Smith, H. V., & Gannon, K. N. (1983). Effects of switching rate and changeover requirement on performance on nondepriving schedules. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 281–291.

Timberlake, W., & Allison, J. (1974). Response deprivation: An empirical approach to instrumental performance. *Psychological Review, 81,* 146–164.

White, J. M. (1985). Schedule-induced wheel-running: Effects of exposure to the schedule. *Physiology and Behavior, 34,* 119–122.

Wollnik, F., & Turek, F. W. (1988). Estrous correlated modulations in circadian and ultradian wheel-running activity rhythms in LEW/Ztm rats. *Physiology and Behavior, 43,* 389–396.